

# Trophic Preferences of Three Soil Macroarthropods (Preliminary Study)

*Jorge P. CANCELA DA FONSECA & Leïla MEZIANE*

Analyse des Systèmes Écologiques, Écologie du Sol, C.N.R.S.  
Université Paris 7, Laboratoire de Biologie végétale et d'Écologie forestière, F-77300 Fontainebleau, France

## ABSTRACT

The main objective of this study is to compare the trophic behaviour of two macroarthropod species belonging to two different invertebrate groups - Diplopoda and Isopoda - but which are, apparently, morphologically similar and have a similar defence, armadillo behaviour (roller species): *Glomeris marginata* (Villers) and *Armadillidium vulgare* (Latreille). *Oniscus asellus* Linné, a clinger species, was also taken into account. These species coexist in the soil of Fontainebleau and Montmorency Forests. They feed on beech, oak and chestnut litter. Three classes of leaf litter were tested out: I. Litter of the year; dark leaves, thick, with few or no rotting spots; II. Old litter; dark leaves, thick but thinner than in I., with light rotting spots; and, III. Old litter; bleached, thin leaves. A Student-t test of the data shows that the three species have a similar trophic behaviour concerning the chestnut litter, but a different one concerning the litter of both beech and oak.

## RÉSUMÉ

### Préférences alimentaires de trois macroarthropodes édaphiques (étude préliminaire).

Le principal objectif de cette étude est de comparer le comportement trophique de deux espèces de macroarthropodes appartenant à deux groupes différents d'invertébrés - Diplopoda et Isopoda - mais qui sont, en apparence, morphologiquement semblables et ont un comportement de défense similaire en se roulant en boule : *Glomeris marginata* (Villers) et *Armadillidium vulgare* (Latreille). *Oniscus asellus* Linné, isopode dépourvu de capacité de volvation, a été aussi pris en compte. Ces espèces coexistent dans les sols des forêts de Fontainebleau et de Montmorency. Elles se nourrissent de litière de hêtre, de chêne et de châtaignier. On a testé trois classes de litière : I. Litière de l'année ; feuilles sombres, épaisses, sans ou avec peu de taches de pourriture blanche ; II. Litière des années précédentes ; feuilles sombres, épaisses, mais plus minces qu'en I., avec des taches claires de pourriture blanche ; et, III. Litière des années précédentes ; feuilles minces, blanchies. L'application aux données du test-t de Student a montré que les individus de ces trois espèces d'arthropodes présentent un comportement trophique similaire en ce qui concerne la litière de châtaignier, mais différent vis-à-vis des litières de hêtre et de chêne.

## INTRODUCTION

The main objective of this study was to compare the trophic behaviour of two soil macroarthropod species belonging to two different invertebrate groups, Diplopoda and Isopoda, but which are, apparently, morphologically similar and have a similar rolling defence, "armadillo" behaviour: *Glomeris marginata* (Villers) and *Armadillidium vulgare* (Latreille). Few studies compare these two macroarthropod species. In general, they compare either the two



isopods *A. vulgare* and *Oniscus asellus* Linné, or the latter species with *G. marginata* (e.g. HARTENSTEIN, 1964; NEUHAUSER & HARTENSTEIN, 1978; HASSALL & RUSHTON, 1984; INESON & ANDERSON, 1985; SUTTON & HARDING, 1989). One of the few authors that compared these two species of isopods with one species of *Glomeris*, not *G. marginata* but *G. connexa* Koch, was DUNGER (1958). However, these three species coexist in the same ecosystem we studied several years ago, a beech woodland: La Tillaie in Fontainebleau Forest (MEZIANE, 1976; CANCELA DA FONSECA & MEZIANE, 1978). This is why *O. asellus* is also taken into account.

Our aim was to study comparatively the ecological niches of two roller species coming from two different arthropod classes (Crustacea and Diplopoda) and their differential roles on the breakdown of forest litter. For this, one of the points was to detail the trophic preferences of such species. This preliminary work presents some significant results related to litter preferences, useful for the comprehension and development of future studies dealing with comparative ecological importance of individuals and populations forming such "functionnal macroarthropod groups".

### MATERIAL AND METHODS

The two roller species studied here are *A. vulgare* (AVU) and *G. marginata* (GMA), and the clinger species, *O. asellus* (OAS).

All were present in both the Fontainebleau and Montmorency Forest ground floors. They feed on litter. Three types of litter were given to them in our experiments: Beech litter (*Fagus sylvatica* Linné - FSY), Oak litter (*Quercus sessiliflora* Salisbury - QSE) and Chestnut litter (*Castanea sativa* Miller - CSA). Three classes of litter were used under the experimental conditions: I. Litter of the year, autumn 1976; dark leaves, thick, with few or no rotting spots; II. Old litter of the years before 1976; dark leaves, thick but thinner than in I., with light rotting spots; and, III. Old litter of the years before 1976; bleached, thin leaves. Five replicates were done with a number of leaves variable according to the number of leaves available in each class. The emphasis was put on the beech litter. The experiments were made at room conditions of about 15-17°C and 80% R.H. from May to November 1977. Each adult, after 48 hours with no food (fasting), was put in contact with each type of litter for a period of 2 days.

The consumption rates (in %) were evaluated by assessing the area of the leaves eaten by each adult in relation to the total leaf area available. The numerical results (Table 1, Fig. 1) were analysed by the Student-t test (Table 2).

### RESULTS

First of all, the three species, but mainly the millipede *G. marginata* and the woodlouse *O. asellus*, have a clear preference to the chestnut litter (classes I, II and III), and a significant avoidance, less for *G. marginata*, of the beech litter of the year (class I). However, the most important antagonistic difference of the feeding behaviour between the millipede *G. marginata* and the woodlouse *A. vulgare* concerns the almost complete avoidance of, respectively, the oak and the beech litter of the year (class I). The same kind of opposition concerned their preferences to the old, thick beech litter (class II). In relation to *G. marginata*, *O. asellus* has a trophic behaviour similar to that of *A. vulgare*, except for the old, thick beech litter (class II).

Furthermore, *A. vulgare* seems to prefer the thick chestnut and oak litter to the beech one (classes I and II), while *G. marginata* seems to prefer the beech litter to the oak litter of the year (class I), the chestnut litter to the oak and the beech litter of the year (class I), and the old, thick chestnut litter to the old, thick beech litter (class II). *O. asellus* prefers the chestnut and the oak litter of the year to the beech one (class I), and the whole old chestnut litters to those of beech (classes II and III).

Comparing the frequency profiles of the data some "odd" data were excluded. This mainly increased the significant differences already observed. However, some significant differences appeared, but above all for the classes with rather few data.



TABLE 1. — Mean consumption rates (%) of litter classes by *Glomeris marginata*, *Armadillidium vulgare* and *Oniscus asellus*.  $\bar{x}$  = Corrected means.

Tree species	Litter classes	<i>G. marginata</i>		<i>A. vulgare</i>		<i>O. asellus</i>	
		No. of leaves	$\bar{x} \pm s \bar{x}$	No. of leaves	$\bar{x} \pm s \bar{x}$	No. of leaves	$\bar{x} \pm s \bar{x}$
<i>F. sylvatica</i>	I	27	36.7 $\pm$ 7.4	28	14.5 $\pm$ 4.0	24	11.8 $\pm$ 2.0
	Ix			25	8.0 $\pm$ 1.9		
	II	36	46.3 $\pm$ 5.8	37	29.3 $\pm$ 4.7	41	43.6 $\pm$ 4.4
	IIx			34	24.6 $\pm$ 3.9	39	45.8 $\pm$ 4.3
	III	6	27.1 $\pm$ 15.5	8	47.8 $\pm$ 11.8	9	53.6 $\pm$ 10.5
	IIIx	5	13.4 $\pm$ 8.9	7	53.8 $\pm$ 11.7	8	60.3 $\pm$ 9.1
<i>Q. sessiliflora</i>	I	8	7.3 $\pm$ 4.7	8	52.2 $\pm$ 10.6	4	48.1 $\pm$ 8.7
	Ix	7	3.0 $\pm$ 2.1	7	58.2 $\pm$ 10.1		
	II	11	54.2 $\pm$ 14.3	11	52.2 $\pm$ 8.9	17	54.4 $\pm$ 7.4
	IIx	9	60.1 $\pm$ 14.7	10	62.7 $\pm$ 8.6	16	57.2 $\pm$ 7.3
	III	6	42.6 $\pm$ 13.8	6	51.2 $\pm$ 15.8	3	64.3 $\pm$ 23.1
	IIIx	5	51.1 $\pm$ 13.3	5	60.9 $\pm$ 15.3	2	87.3 $\pm$ 4.7
<i>C. sativa</i>	I	7	82.1 $\pm$ 7.3	10	56.6 $\pm$ 9.5	10	68.9 $\pm$ 9.1
	Ix			9	51.8 $\pm$ 8.9	9	75.7 $\pm$ 6.6
	II	12	78.1 $\pm$ 8.2	7	66.9 $\pm$ 9.6	4	75.8 $\pm$ 9.6
	IIx	11	85.2 $\pm$ 4.5				
	III	5	76.2 $\pm$ 19.1	7	71.1 $\pm$ 11.4	9	83.5 $\pm$ 7.6
	IIIx	4	95.3 $\pm$ 2.0	8	88.9 $\pm$ 6.1		

## DISCUSSION AND CONCLUSION

In the beech woodland of "La Tillaie" (Fontainebleau Forest) of the three macroarthropod species, *A. vulgare* was dominant (72%) followed by *O. asellus* (15%) and *G. marginata* (13%) (February 1972-January 1973; MEZIANE, 1976). Their coexistence in time and space, measured in terms of "activity behaviour" by pitfall trap method, was more important for *G. marginata* and *A. vulgare* (SCHOENER's index  $R_t=0.636$  and  $R_s=0.746$ ) than for *G. marginata* and *O. asellus* ( $R_t=0.583$  and  $R_s=0.604$ ), while, for *A. vulgare* and *O. asellus*, it was somewhat higher in time ( $R_t=0.652$ ) and lower in space ( $R_s=0.563$ ). Their spatial distribution was also different: more random for *G. marginata* (negative binomial distribution parameter  $k=8.48$ ), more aggregative for *O. asellus* ( $k=0.62$ ), and for *A. vulgare* in between ( $k=3.21$ ). Though the surface of the site studied was not very large, its central part was not covered by herbaceous vegetation, only by beech litter, but their peripheric borders have a great number of mesohabitats, like fallen beech trunks and branches, decayed logs, small grassy patches, several holly bushes, and a small grassland glade. Thus, as the three species were present everywhere and coexist in this site, they can easily overlap part of their ecological niches. Nevertheless, they had some habitat preferences: *G. marginata* for the uncovered litter, *O. asellus* for the decayed wood places, and *A. vulgare* for the grassy patches and the small grassland glade. It is well known that *G. marginata* prefers woodland to grassland soils where it inhabits very often with *A. vulgare*, which prefers them, and that *O. asellus* prefers woodland soils and decayed wood (WARBURG, 1968; WALLWORK, 1976; RUSHTON & HASSALL, 1983; HASSALL & RUSHTON, 1984; SUTTON & HARDING, 1989).

TABLE 2. — Significant trophic preferences between *Glomeris marginata*, *Armadillidium vulgare* and *Oniscus asellus*. In brackets: a) Classes of litter; b) Corrected means. Significance: n.s. = not significant; \* = 0.05>P>0.01; \*\* 0.01>P>0.001; \*\*\* = P<0.001.

Species	Type of preferences	Consumption rates (%)	P<5%
<i>G. marginata</i>	.Over <i>A. vulgare</i> :		
	Thick BEECH litter of the year (I)	36.7 vs 14.5	*
		(36.7 vs 8.0	***)
	Thick, old BEECH litter (II)	46.3 vs 29.3	*
		(46.3 vs 24.6	**)
	.Over <i>O. asellus</i> :		
	Thick BEECH litter of the year (I)	36.7 vs 11.8	**
	.Thick BEECH litter of the year (I)	36.7 vs 7.3	*
	vs thick OAK litter of the year (I)	(36.7 vs 3.0	*)
	.Thin, old OAK litter (III)	42.6 vs 27.1	n.s.
	vs thin, old BEECH litter (III)	(51.1 vs 13.4	*)
	.Thick CHESTNUT litter of the year (I)	82.1 vs 36.7	**
	vs thick BEECH litter of the year (I)		
	.Thick, old CHESTNUT litter (II)	78.1 vs 46.3	**
	vs thick, old BEECH litter (II)	(85.2 vs 46.3	***)
	.Thin, old CHESTNUT litter (III)	76.2 vs 27.1	n.s.
	vs thin, old BEECH litter (III)	(95.3 vs 13.4	***)
<i>A. vulgare</i>	.Thick CHESTNUT litter of the year (I)	82.1 vs 7.3	***
	vs thick OAK litter of the year (I)	(82.1 vs 3.0	***)
	.Thin, old CHESTNUT litter (III)	76.2 vs 42.6	n.s.
	vs thin, old OAK litter (III)	(95.3 vs 51.1	*)
	.Thick, old BEECH litter (II)	46.3 vs 27.1	n.s.
	vs thin, old BEECH litter (III)	(46.3 vs 13.4	*)
	.Thick, old OAK litter (II)	54.2 vs 7.3	*
	vs thick OAK litter of the year (I)	(60.1 vs 3.0	***)
	.Thin, old OAK litter (III)	42.6 vs 7.3	*
	vs thick OAK litter of the year (I)	(51.1 vs 3.0	**)
Species	Type of preferences	Consumption rates (%)	P<5%
<i>A. vulgare</i>	.Over <i>G. marginata</i> :		
	Thick OAK litter of the year (I)	52.2 vs 7.3	***
		(58.2 vs 3.0	***)
	Thin, old BEECH litter (III)	47.9 vs 27.1	n.s.
		(53.8 vs 13.4	*)
	.Thick OAK litter of the year (I)	52.2 vs 14.5	***
	vs thick BEECH litter of the year (I)	(58.2 vs 8.0	***)
<i>O. asellus</i>	.Thick, old OAK litter (II)	52.2 vs 29.3	**
	vs thick, old BEECH litter (II)	(62.7 vs 24.6	***)



<i>A. vulgare</i> (continued)	.Thick CHESTNUT litter of the year (I) vs thick BEECH litter of the year (I)	56.6 vs 14.5 (51.8 vs 8.0)	*** ***)
	.Thick, old CHESTNUT litter (II) vs thick, old BEECH litter (II)	66.9 vs 29.3 (66.9 vs 24.6)	** ***)
	.Thick, old BEECH litter (II) vs thick BEECH litter of the year (I)	29.3 vs 14.5 (24.6 vs 8.0)	* **)
	.Thin, old BEECH litter (III) vs thick BEECH litter of the year (I)	47.8 vs 14.5 (53.8 vs 8.0)	** ***)
	.Thin, old BEECH litter (III) vs thick, old BEECH litter (II)	47.8 vs 29.3 (53.8 vs 24.6)	n.s. **)

Species	Type of preferences	Consumption rates (%)	P<5%
<i>O. asellus</i>	.Over <i>G. marginata</i> :		
	Thick OAK litter of the year (I)	48.1 vs 7.3 (48.1 vs 3.0)	** ***)
	Thin, old BEECH litter (III)	53.6 vs 27.1 (60.3 vs 13.4)	n.s. **)
	.Over <i>A. vulgare</i> :		
	Thick, old BEECH litter (II)	43.6 vs 29.3 (45.8 vs 24.6)	* ***)
	.Thick OAK litter of the year (I) vs thick BEECH litter of the year (I)	48.1 vs 11.8	***
	.Thick CHESTNUT litter of the year (I) vs thick BEECH litter of the year (I)	68.9 vs 11.8 (75.7 vs 11.8)	*** ***)
	.Thick, old CHESTNUT litter (II) vs thick, old BEECH litter (II)	75.8 vs 43.6 (75.8 vs 45.8)	* *)
	.Thin, old CHESTNUT litter (III) vs thin, old BEECH litter (III)	83.5 vs 53.6 (88.9 vs 60.3)	* *)
	.Thick CHESTNUT litter of the year (I) vs thick OAK litter of the year (I)	68.9 vs 48.1 (75.7 vs 48.1)	n.s. *)
	.Thick, old BEECH litter (II) vs thick BEECH litter of the year (I)	43.6 vs 11.8 (45.8 vs 11.8)	*** ***)
	.Thin, old BEECH litter (III) vs thick BEECH litter of the year (I)	53.6 vs 11.8 (60.3 vs 11.8)	*** ***)
	.Thin, old OAK litter (III) vs thick OAK litter of the year (I)	64.3 vs 48.1 (87.3 vs 48.1)	n.s. *)

Fontainebleau Forest is mainly a beech-oak forest while Montmorency Forest has also chestnut woods. This is why our experimental trophic research concerned principally beech litter and secondly oak and chestnut litter. Laboratory results showed significant trophic differences between the three macroarthropod species in relation to the consumption rates of beech and oak litter. No significant differences being observed in relation to the consumption rates of chestnut litter. Thus, the pill millipede, *G. marginata*, avoids the thick oak litter of the year (which was also observed by GEOFFROY *et al.*, 1987) more intensely than the two woodlice, *A. vulgare* and

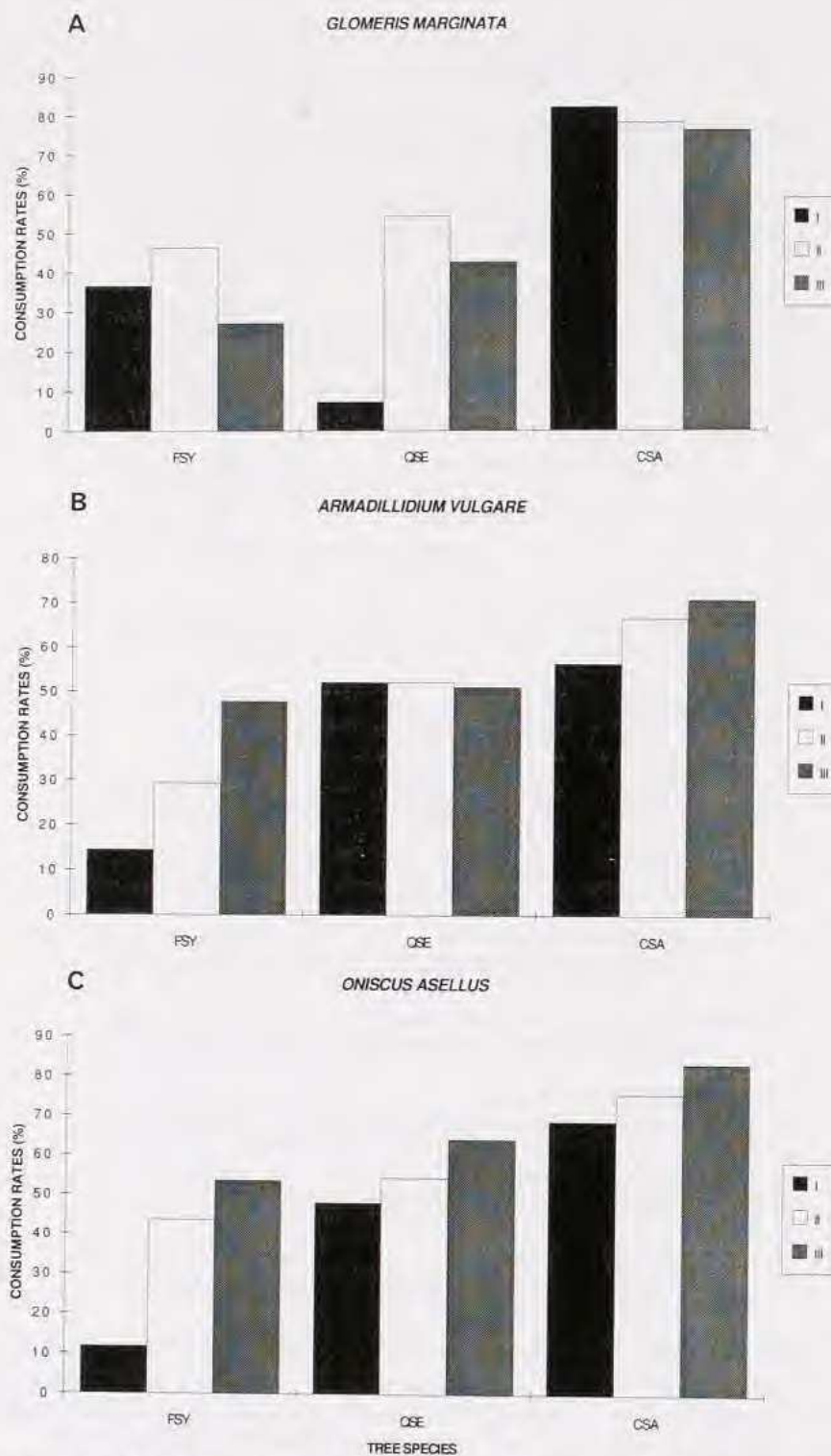


FIG. 1. — Consumption rates (%) of three classes of litter (I, II, III) by one pill-millipede (*G. marginata*) and two woodlice (*A. vulgare* and *O. asellus*) adult individuals fed on *Fagus sylvatica* (FSY), *Quercus sessiliflora* (QSE) and *Castanea sativa* (CSA) leaves.



*O. asellus*, avoid the thick beech litter of the year. These two species have a similar trophic behaviour against that of *G. marginata* behaviour which is also showed by their preferences to the thin, old beech litter. However, some significant differences were observed between them, *O. asellus* preferring the thick, old beech litter more than *A. vulgare*. Moreover, the three species prefer the chestnut litter to the other types of litter. Though, this was also observed by ANDERSON (1973), it seems no to be directly attributable to the nitrogen contents, the C/N ratio or even the polyphenol contents of the leaf litter. The same was pointed out by NEUHAUSER & HARTENSTEIN (1978) which indicates however that *Fagus* and *Quercus* litter are "scarcely palatable" to *A. vulgare* and *O. asellus*. Nevertheless, BECK & BRESTOWSKY (1980) say that *O. asellus* grew better on freshly fallen leaves of beech and oak than on overwintered ones which contradicts DUNGER (1958) and PIEARCE (1989) observations. In our essays, they preferred significantly the thick oak litter of the year to the thick beech litter of the year, contrary to *G. marginata*. It seems, however, that the pill millipede is not very common on the beech woods (WALLWORK, 1976), but more common in mixed beech-oak woodlands when oak leaves form part of the litter (VAN DER DRIFT, 1951). In any case, all species preferred old litter to freshly fallen one. The freshly fallen leaves have normally high polyphenol, like lignin, and tannin contents which inhibit their feeding by the animals (MILLER & CAMERON, 1983; RUSHTON & HASSALL, 1983; HASSALL & RUSHTON, 1984; GUNNARSSON, 1987; MOCQUARD *et al.*, 1987; JAMBU *et al.*, 1988).

Besides, it is well known that microorganisms are able to degrade the phenolic and tannin compounds of the leaves, and by that way to render them more palatable to the animals (DUNGER, 1958; HASSALL & RUSHTON, 1984; GUNNARSSON, 1987; BIGNELL, 1989). This can justify the preferences for the old litter, but the preferences for the litter of the year need a more detailed biochemical research.

#### REFERENCES

- ANDERSON, J. M., 1973. — The breakdown and decomposition of sweet chestnut (*Castanea sativa* Mill.) and beech (*Fagus sylvatica* L.) leaf litter in two deciduous woodland soils. II. Changes in carbon, hydrogen, nitrogen and polyphenol content. *Oecologia (Berl.)*, **12** : 275-288.
- BECK, L. & BRESTOWSKY, E., 1980. — Auswahl und Verwertung verschiedener Fallaubarten durch *Oniscus asellus* (Isopoda). *Pedobiologia*, **20** : 428-441.
- BIGNELL, D. E., 1989. — Relative assimilation of <sup>14</sup>C-labelled microbial tissues and <sup>14</sup>C-plant fibre ingested with leaf litter by *Glomeris marginata* under experimental conditions. *Soil Biol. Biochem.*, **21** : 819-827.
- CANCELA DA FONSECA, J. P. & MEZIANE L., 1978. — Macroarthropodes : abondance relative et activité saisonnière de quelques groupes (Isopodes, Diplopodes, Chilopodes et Opilions). [In : LEMÉE G., La hêtraie naturelle de Fontainebleau.] In : F. BOURLIÈRE & M. LAMOTTE, *Problèmes d'Écologie : Structure et fonctionnement des écosystèmes terrestres*. Paris, Masson : 116-119.
- DUNGER W., 1958. — Über die Zersetzung der Laubstreu durch die Boden-Makrofauna im Auenwald. *Zool. Jb. (Syst.)*, **86** : 139-180.
- GEOFFROY, J. J., CÉLÉRIER, M. L., GARAY, I., RHERISSI, S. & BLANDIN, P., 1987. — Approche quantitative des fonctions de transformation de la matière organique par des Macroarthropodes saprophages (Isopodes et Diplopodes) dans un sol forestier à moder. *Protocoles expérimentaux et premiers résultats. Rev. Ecol. Biol. Sol*, **24** : 573-590.
- GUNNARSSON, T., 1987. — Selective feeding on a maple leaf by *Oniscus asellus* (Isopoda). *Pedobiologia*, **30** : 161-165.
- HARTENSTEIN, R., 1964. — Feeding, digestion, glycogen and the digestive system in *Oniscus asellus*. *J. Insect Physiol.*, **10** : 611-621.
- HASSALL, M. & RUSHTON, S. P., 1984. — Feeding behaviour of terrestrial Isopods in relation to plant defenses and microbial activity. *Symp. zool. Soc. London*, **53** : 487-505.
- INESON, P. & ANDERSON, J. M., 1985. — Aerobically isolated bacteria associated with the gut and faeces of the litter feeding macroarthropods *Oniscus asellus* and *Glomeris marginata*. *Soil Biol. Biochem.*, **17** : 843-849.
- JAMBU, P., JUHAULT, P. & MOCQUARD, J. P., 1988. — Étude expérimentale de la contribution du crustacé isopode *Oniscus asellus* à la transformation des litières forestières sous chêne sessile. *Pedobiologia*, **32** : 147-156.
- MEZIANE, L., 1976. — Activité saisonnière de quelques groupes de Macroarthropodes. Mémoire de DEA d'Écologie animale, Université Paris VI, 54 pp.

- MILLER, R. H. & CAMERON, G. N., 1983. — Intraspecific variation of life parameters in the terrestrial Isopod, *Armadillidium vulgare*. *Oecologia (Berl.)*, **57** : 216-226.
- MOCQUARD, J. P., JUCHAULT, P., JAMBU, P. & FUSTEC, E., 1987. — Essai d'évaluation du rôle des crustacés oniscoïdes dans la transformation des litières végétales dans une forêt feuillue de l'ouest de la France. *Rev. Ecol. Biol. Sol*, **24** : 311-325.
- NEUHAUSER, E. F. & HARTENSTEIN, R., 1978. — Phenolic content and palatability of leaves and wood to soil isopods and diplopods. *Pedobiologia*, **18** : 99-109.
- PIEARCE, T. G., 1989. — Acceptability of pteridophyte litters to *Lumbricus terrestris* and *Oniscus asellus*, and implications for the nature of ancient soils. *Pedobiologia*, **33** : 91-100.
- RUSHTON, S. P. & HASSALL, M., 1983. — Food and feeding rates of terrestrial isopod, *Armadillidium vulgare* (Latreille). *Oecologia (Berl.)*, **57** : 415-419.
- SUTTON, S. L. & HARDING, P. T., 1989. — Interpretation of the distribution of terrestrial Isopods in the British Isles. *Monitor. Zool. ital. (N.S.) Monogr.*, **4** : 43-61.
- VAN DER DRIFT, J., 1951. — Analysis of the animal community in a beech forest floor. *Tijdschr. Ent.*, **94** : 1-168.
- WALLWORK, J. A., 1976. — *The distribution and diversity of soil fauna*. London, Academic Press, 355 pp.
- WARBURG, M. R., 1968. — Behavioural adaptations of terrestrial isopods. *Am. Zool.*, **8** : 545-559.